ADAPTATION THROUGH NATURAL SELECTION AND ORTHOGENESIS[1]

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Mr. President, Members of the Society, and Friends:
When the president of our society, Professor Conklin, asked me to open this discussion, he suggested that I speak in advocacy of natural selection as the dominant factor in adaptation, saying that several speakers would follow who would attack this conception. As I understand it, a paper in advocacy of natural selection is desired not so much that it may be a target at which following speakers may direct their shafts, as that this conception may not stand without defenders.

It involves some temerity to speak to an audience of American naturalists upon natural selection, for the conception is more than a decade old. It dates even from the dark ages of the middle of the last century, and we naturalists, like the Athenians to whom Paul spoke, are continually seeking some new thing. I can not even, as DeVries and Bateson in the case of Mendel's principles, claim the honor of a re-discoverer, for through all the years since its first promulgation the conception of natural selection has been constantly to the fore and has been discussed and re-discussed until many, I fear, have wearied of it, and for this very reason may be ready to give too undiscriminating welcome to other conceptions that seek to supplant the old idea.

[1] Read at the Symposium on Adaptation at the meeting of the American Society of Naturalists, Cleveland, January 2, 1913.

There are two sets of factors in producing and determining the direction of evolution, those within the organism, and those external to it. In earlier studies of evolution the external factors received by far the most attention, and only recently have the internal factors begun to receive the thought they deserve. Of the external factors, natural selection is the one for which the largest claims have been made and the one whose claims have been most cordially allowed. I think, however, there are few, if any, of us who do not feel that some of the advocates of natural selection have gone too far. Wallace, for example, would not allow that there are any characters of animals or plants which are not useful to their possessors and have not been perpetuated and emphasized because of this usefulness. Admitting, as we must, that we know but little of the intimate life of organisms, and that the use of many really most useful characters may fail to impress us only because of our ignorance of real conditions, still I think most of us feel not only that the claim that all structures and qualities of organisms are useful is an exaggerated claim, but that very many characteristics are either of indifferent quality, or are so slightly useful as not to be of selection value, or even are slightly disadvantageous. The more closely one studies any organism the more will he become impressed with the number of these non-useful or doubtfully useful qualities, and close and careful students are likely to find their vision of natural selection grow dim, like the pilgrim who, in the midst of the woods, could not see the forest for the trees.

But as we view organic nature in its wider aspects is there any other feature so prominent as the adaptation of organisms to their environment and to the lives they must live in the midst of this environment? However many details of structure or behavior may fail to show their utility, still it remains true that there is no phenomenon of organic nature more impressive than adaptation.

In our study of evolution we have, then, this thing to explain—namely, the universal prevalence of a high degree of adaptation of organisms in habit, function and structure, to their environment, and yet the presence of

many qualities, for the most part minor qualities, which so far as we can judge, are non-adaptive. I would suggest for your consideration the propositions that the broader adaptive features are due to natural selection, and that the non-adaptive minor characters are the result partly of factors within the organism, and partly of external factors other than natural selection. This paper will not refer further to these other external factors, but will discuss one of the factors within the organism.

Evidence accumulated during the last decade seems to indicate that fluctuating variations are not significant, and that only mutations are stable and can serve as a foundation for evolution. Perhaps we have accepted this statement a little too hastily. The actual evidence in its favor is not all that could be desired, but it seems to be the general opinion to-day. If this opinion is well founded, it is through the study of the origin and nature of mutation that we may hope to gain most light upon the problem of the origin of adaptation.

When one comes to think of it, we really know very little of mutation. Few instances have been carefully observed and recorded. But in the midst of this scant knowledge of mutation one fact stands out clearly, that mutation apparently is not indeterminate, occurring in all directions equally, and changing from generation to generation, as would be the case were it purely fortuitous. Our best studied instances of mutation are still seen in *Œnothera lamarckiana,* and in all the observations upon the mutation of this species nothing is more patent than that there are certain definite tendencies for particular mutants of very complex and very clearly recognizable types to appear generation after generation, in numbers that are very much greater than could be accounted for by any chance aggregation of unit characters to make these few well-marked types.

In 1905 I wrote as follows:

In the Amsterdam Garden the mutant *albida* appeared in four different generations from *lamarckiana* parents, previous to 1902, 15 *albida* appearing in one generation, 25 in another, 11 in another and 5 in another. *Nanella* appeared 5 times in one generation, and in other

generations, respectively, 3, 60, 49, 9, 11 and 21 times. *Lata, oblonga, rubrinervis* and *scintillans* appeared frequently.

In the fourth generation, along with 14,000 *lamarckiana* plants, there appeared 41 *gigas*, 15 *albida*, 176 *oblonga*, 8 *rubrinervis*, 60 *nanella*, 63 *lata* and 1 *scintillans*, all bred from *lamarckiana* seed. In the fifth generation, similarly bred from pure *lamarckiana* seed, among 8,000 *lamarckiana* plants were found 25 *albida*, 135 *oblonga*, 20 *rubrinervis*, 49 *nanella*, 142 *lata* and 6 *scintillans*. In the fourth generation one plant in 80 was *oblonga*. In the fifth generation one plant in 60 was *oblonga*. DeVries himself says: " A species therefore, is not born only a single time, but repeatedly, in a large number of individuals and during a series of consecutive years.

Oblonga differs from the parent species *lamarckiana* not in a single feature, but in an elaborate complex of characters. The other mutants likewise are distinguished from *lamarckiana* by a complex of characters rather than by a single feature.

The mutation can hardly be entirely fortuitous if, for several generations, out of every thousand offspring of pure *lamarckiana* parents, there appear more than ten plants marked by the particular complex group of characters which designate *oblonga*. Were *oblonga* demarcated from *lamarckiana* by but a single character, it would be remarkable to find it appearing repeatedly and in such numbers. When we remember that it is defined by an extensive series of characters differentiating it from *lamarckiana* and from all other mutants observed, are we not led to the conclusion that mutation in *Œnothera lamarckiana* is not wholly fortuitous, but is to a degree predetermined; and that there is some tendency to the production of the *oblonga* and other types in numbers much greater than would be secured by purely fortuitous and indeterminate mutation?

Mutation in our most carefully observed instance, therefore, is clearly determinate. There is in *Œnothera lamarckiana* a tendency to mutate in certain definite directions generation after generation. This trend to mutation in certain particular directions is an example of a condition within the organism which might decidedly affect the course of the future evolution of this *Œnothera* and its descendants.

But we can safely go further. Not only have we evidence that there exist tendencies to produce certain mutants repeatedly, paleontological records show, I believe, that there have existed trends toward an increasing emphasis upon certain characters and that these trends, in some instances at least, lay along lines that produced no more perfect adaptation of their possessors to their environment.

Neumayr's well-remembered figures of fossil *Paludinas* from Slavonian lake deposits show an increasing rugosity of shell and irregularity of aperture, but the separate steps of this change could hardly have been of selection value and have occurred under the control of natural selection. One is irresistibly drawn to believe that there was in these *Paludinas* an internal tendency to mutate from generation to generation toward increasing rugosity of the shell and increasing irregularity of its aperture.

Similar trends in the development of limb and tooth structure of the horse were long ago emphasized by American paleontologists. There is no conceivable utility in the modified shell form of the *Paludina*, and, in the case of the horse, the wonder is that the race has not long ago been exterminated. Among the Cephalopods are some forms which show most complex patterns of the partitions. There are complete intergrading stages shown in the known species between simple suture lines and the most fantastically fimbriated. There seems here, again, to be evidence of a trend toward increasing convolution of the sutures, rather than evidence of the appearance of a useful character and its increase by successive steps each of selection value. In a somewhat similar way, over-ornamentation and bizarre character developed in the Trilobites by steps which can hardly be imagined useful. Many such examples might be cited.[2]

It may seem that I am arguing against the importance of natural selection, but I think I am not, and for this reason: the very trends, of whose existence I think we have good evidence, are themselves subject to natural selection, and if they are in hurtful directions, they will ultimately cause the extermination of the species exhibiting them. I very much doubt if such a monstrosity as the horse could long persist, except for man's aid, for it

[2] On the afternoon of the day when this paper was read Professor B. M. Davis reported that among the offspring of his *Œnothera* hybrids were some mutants with flowers larger than either parent species, and that for two generations (as far as his experiments went) the flowers increased in size. This is apparently an example of just such a trend in mutation as I have indicated above.

is about the least adaptable beast we know. The Cephalopods with complex partitions have all perished. The bizarre Trilobites similarly persisted each for but a brief period.

I would not claim that the over-ornamentation in these cases was the cause of extermination. It seems more probable that it is merely one noticeable indication of a general unbalanced condition of the organism, a condition affecting probably function as well as structure. I suspect that more species have perished because of physiological maladjustment than from any disadvantageous structural qualities.

In quatenary times in numerous species, great emphasis seems to have been laid upon bulk and the very hugeness of some of these species probably aided in their extermination.

Non-adaptive qualities, when first appearing, may often be comparatively harmless, at least may not be sufficiently hurtful to lead to the extermination of the species in which they appear. But qualities comparatively innocent in their beginnings, when over-emphasized by such trends as we are discussing, may go beyond the limit that even long suffering nature will allow and extermination follow. The goblin of natural selection will get him in the end if he doesn't watch out. It is a case of giving the species rope enough and letting it hang itself. Instead, therefore, of supplanting natural selection, such orthogenesis as this really acts in the end to aid in eliminating many species whose characters in their beginnings were indifferent, natural selection finally dominating and compelling adaptation.

Since mutation-trends in helpful directions will be aided by selection, through the destruction of the rivals of their possessors, while hurtful trends will cause extermination, we see that natural selection has a determinative influence upon the direction of evolution, steering the species along safe paths of progress.

Further advance in the study of the method of evolution may be expected from the study of trends in mutation. Such study should be continued for many years,

breeding in great numbers for many generations from some highly mutating stock. Such work can not well be undertaken by a single individual, for it should continue through several human generations. It should be undertaken by some institution which will ensure the endurance of the investigation beyond the present generation. Possibly the best object for such study would be the Syracuse Trilliums—*Trillium grandiflorum*—whose remarkable variation Britcher[3] has so well described. Variation in these Syracuse Trilliums is more universal and more extensive than in any other plants or animals I know. It is so great that it can hardly be of the fluctuating type. It is, in all probability, true mutation, and if so it offers the best opportunity I know for the study of the phenomena of mutation.

SUMMARY

Organisms show adaptation in their more important characters, while many of their minor characters fail to show their utility.

There are definite tendencies to mutation in particular directions, and there is abundant paleontological evidence of trends toward increasing modification in particular directions.

Qualities so appearing may be indifferent in their beginnings, but may through this orthogenesis become sufficiently useful or hurtful to affect selection. Such trends, when they affect physiological qualities, are likely to bring about an unbalanced, distorted physiological condition and be peculiarly hurtful. Probably this has been one of the chief causes of the disappearance of species.

Orthogenesis as thus interpreted is but the handmaiden of natural selection which, acting upon all qualities thus developed to major proportions, will cause them to disappear if ill-adapted. At the same time advantageous trends will be encouraged in the struggle for existence and the direction of evolution be turned toward further adaptation.

Adaptation is the most salient result of evolution and natural selection its great cause.

[3] H. W. Britcher.

ADAPTATION IN THE LIVING AND NON–LIVING[1]

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The fundamental differences in concept and mode of thought, which may be remarked between the sciences of the living and those of the non-living, are perhaps nowhere better exemplified than in the interpretations and in the degree of prominence which they respectively give to the idea of adaptation. A general survey of the natural sciences results in the somewhat startling discovery that biology is the only one of these which deals conspicuously with this idea. I have, therefore, been led to take, for my present paper, the somewhat bizarre title wh'ch has been announced, and I shall here attempt partially to set forth some characteristics and implications of the biological concept of adaptation, and, in certain respects, to compare these characteristics and implications with those of similar concepts which have the place of adaptation in the sciences of the non-living. The term adaptation is used in a passive and in an active sense. I shall consider the two sorts of adaptations in order.

Passive Adaptations.—Adaptations are characteristics, properties or qualities attributable to natural objects. They imply, however, not only mere qualities, but also the presence or absence, in the object considered, of *potentialities* or *capabilities* to be or to do certain things under certain conditions. The term always lays stress on potentialities but it does not imply at all that these are, or have been, realized. If they were actually realized, it would amount to a redundancy to note the existence of the adaptations at all; an adaptation "caught in the act," an already realized potentiality, is so self-evident that we do not need to mention it as such. In such a

[1] Read at the Symposium on Adaptation at the meeting of the American Society of Naturalists, Cleveland, January 2, 1913.

case, the statement of the realization implies the potentiality, for an object is obviously adapted to doing and being what it does and is.

However, doing and being are only relative, for any object may change its state more or less effectively and may possess attributes in different degrees, and our interest in realized potentialities lies not in the *fact,* but in the *degree* of adaptation. Furthermore, the degree of adaptation depends clearly upon the extent to which the object considered possesses those properties or qualities about which our idea of adaptation centers, and so attention is at once turned to the properties or qualities as such.

I may draw an illustration of actually observed adaptations from the science of geology, which perhaps interests itself as much in the survival and distribution of rock masses as does biology in the survival and distribution of living things. My example has to do with the natural selection and distribution of certain boulders and pebbles in a deep Californian valley.

At the time of the filling of the Salton sink by the unruly Colorado River, the only loose stones of the inundated area that were able to keep themselves in contact with the air were fragments of pumice. These were adapted to float upon water, and they largely refused to be submerged. With the rising waters they also rose, and thus were able to take advantage of air movements to redistribute themselves. Had it not been for the floating adaptation, these pumice pebbles would have suffered temporary extinction in the form of submergence, and they would not have been able to survive and to gain dominance in the pebble population of certain Salton beaches which they forthwith proceeded to invade. We have reason to believe that this sort of spontaneous migration of pumice pebbles has taken place many times before in the Salton valley, at periods and seasons when edaphic and climatic conditions happened to favor such readjustments of the tension lines, and that the present

distribution of these curiously endowed stones has been largely brought about through their possession of the floating adaptation.

Probably a geologist would not mention adaptation in this connection; he might succinctly state the apparent specific gravity of pumice, and might then proceed to present the case in terms of this internal character and in terms of more or less quantitatively known features of the surroundings; for the idea of adaptation here takes account of the low specific density of the rock and the ability to float upon water implied thereby, and to state that pumice is adapted to float is redundant, after we know its specific density. For aught I know also, there may be different species of pumice, some of which might be observed to float higher or a longer time upon water, and in such case, what we might term the varying degrees of adaptation in the different species should be quantitatively brought out—and then dismissed—by an adequate study of the internal qualities of the rocks.

But not nearly all of the potentialities discoverable in natural objects are of this realized, and consequently directly observable sort. The future is no doubt pregnant with hitherto untested adaptations and our imagination frequently suggests these as problems. Of course modern natural science responds to the proposal of this sort of adaptation, *try it and see if it is true,* and many of us are busy just now in doing this very thing.

If we find observational proof of the suggested property, interest in its adaptational aspect fades, for the case then passes over into my first category, of actually observed adaptations. Also, the experimental test of a proposed potentiality—as to whether it is attributable or not to the object considered—is but a case of observation, properly prepared for. Not readily finding the necessary conditions and the object together in nature, we find them separately (at different places or times) and proceed to bring them together. Thus my first experience of the Salton valley was had at a time when it contained

little or no visible water. Let us suppose that interest
was at that time aroused in the distribution of pumice
pebbles upon certain areas of the dry valley floor, and let
us suppose that a previous migration of these, similar to
the one just described, was suggested as a possibility.
At that time the direct test by observation was not pos-
sible, but the whole question—as far as the floating adap-
tation is concerned—could have been settled readily
enough either by bringing water to the pebbles or by
taking some of the pebbles to water. But of course we
should have been dealing, in this instance again, with the
determination of the presence or absence of a certain
property in the pebbles, as related to a certain property
of water.

In the vast majority of the cases of this sort that at-
tract our attention at the present time, however, natural
science is unable to obtain direct observational tests, even
of the experimental sort, and some indirect method of
comparison must be resorted to. Now, indirect methods
for determining the degree of a proposed adaptational
property consists in nothing more than the determina-
tion, by whatever means may be convenient, of the de-
gree to which this property exists in the object consid-
ered. Thus, without ever bringing water and pumice to-
gether, it is perfectly possible to establish the ability of
the latter to float, as by determining the comparative
weights of equal volumes of the two substances.

From what has preceded it is suggested that every
passive adaptation that we may consider resolves itself,
upon adequate analysis, into a problem of the measure-
ment and quantitative comparison of qualities or proper-
ties of objects. If neither the direct experimental test
nor the requisite measurements can be carried out, then
the suggestion of an adaptation is no different from the
statement of any other problem for which no method of
attack has yet been devised. But it must be recognized
in this connection that the usual biological adaptation is
not always appreciated as a problem in comparative

measurement, and that its proposal, especially if made by one in an authoritative position, is far too apt to be received as a declaration rather than as a question. Thus, for example, our elementary texts may tell the innocent beginner that brightly colored flowers are better adapted to fertilization by insects than are their less gaudy neighbors, and without critical analysis, a very complex and exceedingly difficult problem is at once regarded as solved. As a matter of fact, this problem involves comparative measurements for which methods have not yet been devised, so that the cautious biologist must regard the question of this proposed adaptation as utterly beyond us for the present.

Apparently possible potentialities which have not been actually observed in nature, or which have not a basis in quantitative comparisons so as to be possible of definite establishment or refutation, have not played an important rôle in the modern development of the sciences of the non-living, and consequently the adaptational aspect of the qualities of natural objects is seldom mentioned in these sciences. The relative ease with which the qualities of the non-living may now be analyzed into fundamental concepts renders the use of any other terms than those of matter and energy quite out of place in their serious discussions. On the other hand, biological inquiry has still much to do with theoretical attributes which can not be put to any satisfactory test, and this condition may be in part responsible for the prevalence of the adaptational point of view in our science. It seems to be partly because biological problems are too complex for ready analysis at present, that the adaptational properties of living things are so often stated in terms other than those of the fundamental concepts of matter and energy.

In this connection it is, however, to be remembered that ease of analysis depends as much upon the state of the analyzing mind as upon the complexity of the analyzed object. A mind is conceivable, I think, that would con-

sider the phenomenon of cell division as just as capable
of analysis as is that of a chemical reaction like flame;
and we are sure that there have been in the past (and are
indeed at present) minds to which flame would appear
quite as hopeless of analysis as does cell division to us.
I have said that the qualities of living things are too
complex for analysis at present, I might as well have
said that we are at present too ignorant and too feeble to
analyze such qualities. Our science is young yet, not in
years, perhaps, nor yet in absolute achievement, but in
the relation of its present phase of development to the
task which is set before it. It appears to be this youth-
ful quality in biology which may partially explain, as I
have said, the somewhat startling generalization with
which we began.

Active Adaptations.—Biological writing employs the
term adaptation in an active sense as well as in the pas-
sive one heretofore considered in this paper, and it re-
mains to give some attention to this usage, and to an ap-
parent confusion of cause and effect which is connected
therewith. To obtain a clearly legitimate case of active
adaptation we shall have to turn to human affairs, for
reasons which will soon be evident, and the familiar
adaptation of the watch will serve our need as well as
any other. The little machine is complex, too complex
for most of us to understand, and it seems to be much
better adapted than any living thing to long-continued,
uniform motion of a certain specified kind. If I make in-
quiry regarding the causes, or antecedent conditions, to
which this adaptation is due, I find that the various parts
have been made and assembled with reference to the very
adaptation which I am investigating. In my search after
causal relations I have been entrapped in a mesh of un-
investigated psychological phenomena and have discov-
ered the puzzling truth that the watch is what it is,
simply because *it was to be what it is!* In other words,
the cause of the effect which we are considering is re-
garded as some sort of disembodied spirit of the effect

itself, and this effect, in order to be the cause of itself must have existed before it came into being.

Of course we realize that we have thus come into contact with the darkest problem with which biological science has to deal, namely, the problem of human purposeful action and of the human will. While I see no reason for doubting that this problem may eventually yield to analysis and comparative measurements, yet it must be admitted that progress in this direction has only just begun, so that anything but the most superficial considerations in this connection is at present but waste of time and trouble. We have here, for the present, to acknowledge our fundamental ignorance, and to hold our minds in that state of suspended judgment to which, in less complex affairs, students of all the natural sciences have become used.

Although we are as yet unable to analyze into simple terms of matter and energy the antecedents which conditioned the adaptation that is before us in the watch, yet it seems that our analysis of the universe about us has progressed far enough so that we may be justified in frankly maintaining that the problem of purposeful causation has no place in any of our considerations, excepting solely those wherein human consciousness has been involved among the causal conditions. To employ other terms, I think we are bound to regard the nature of the future outcome of all processes as totally non-existent, and consequently absolutely without influence in the present, excepting alone (and temporarily) those processes for which the human will is accounted a necessary antecedent.

We may now inquire as to the causes which have been in operation to bring about the peculiarly low specific gravity of the pumice pebbles in my case of the floating adaptation of these bodies. We are assuredly unable to state these causal conditions in anything approaching completeness, but we are nevertheless sure that human purposefulness has played absolutely no part in the

matter, so that we put the floating adaptation of these pebbles entirely out of mind as soon as we begin our search for the causes thereof.

Geology, it seems, does not find purposeful action necessary in its explanations. Neither does any progress come from a consideration of purposeful changes in the readjustments of atoms with which chemistry deals, nor in the phenomena of heat migration which constitute a portion of the field of physics. Modern astronomy sees no purposeful activity in the motions of sidereal space, nor does meteorology seek in the effects of a storm any suggestion of the causes which brought it into being. Many branches of biological science, however, although confessedly not dealing with human purposeful activity, seem frequently to seek in the future the causes of the present. Thus our science teems with purposeful reactions, and this feature of the idea of adaptation adds its influence to the ones already mentioned, playing an important rôle in keeping the sciences of the non-living essentially and fundamentally separate from those of the living.

The history of the idea of causation in the natural sciences suggests much that may have a bearing on our judgment as to whether this present distinction between the two groups of sciences is necessary and permanent or merely temporary and passing. To primitive man all problems were too complex for adequate analysis, and purposeful activities of many kinds were devised to explain not only the doings of his fellow men but also the doings of all nature. The whole world was then a world of teleological causation. The heavenly bodies moved and the chemical elements combined or separated according to the capricious wills of innumerable deities and demons. Men then heard in the howling of the storm and in the rumble of the earthquake the terrible voices of the spirits of the air and earth. All living things were endowed with a man-like consciousness and power of willing to do, and everything struggled with everything else in a never-ending conflict of capricious wills.

In the development of our race, however, an increasing experience of deterministic causal relations has been accompanied by a progressive effort to expunge the idea of purposefulness from our thinking. The numerous mythological personages just called to mind have gradually suffered a curtailing of their powers for good and evil, and have, in general, by natural science at least, been totally discarded. Many relics of the past of course remain in all our mental life; many of our words and not a few of our instinctive modes of thought are survivals from the teleological period of our development. Jupiter and Venus still play their part in modern astronomy, and Vulcan's name is still heard among geologists. But obvious teleological expressions have been generally outgrown and discarded by all of the sciences that deal with the non-living. In biology alone they persist, mainly as personifications of plants and animals, making our modern writings a curious jumble of exactly stated observations and conclusions, together with many statements that might have been taken bodily from primitive fairy-tales. Foreseeing of the future and conscious purpose are apparently attributed to living things in which we have no evidence for the existence of consciousness. The eye develops in the animal *in order that* it may see, the leaves of the plant are *for the purpose* of obtaining carbon dioxid from the atmosphere. The list of such statements might be made very long, but you are quite familiar with their nature.

Not only are the organisms with which we deal frequently personified to the extent of attributing to them the foresight and will needed to carry out complicated plans, but they are also frequently supposed to be capable of making *a mistaken judgment*. I find in Gibson's translation of Jost's "Plant Physiology," 1907 (page 389), an excellent example of this assumption, where it appears that one lower organism may be clever enough to outwit another. The statement in question reads, "The gall, for example, is of service only to the insect,

but is highly disadvantageous to the plant; we must assume, indeed, by way of explanation, that the insect succeeded in deluding the plant, so that instead of treating the insect as an enemy and an intruder it behaved towards it as if it were a bit of itself.''

I think it is perfectly clear that the non-biological sciences have all passed through a much earlier stage in which purposeful adaptations were seriously considered, and it seems quite as clear that such concepts are not any longer accepted in the serious studies of these sciences. There seems also to be no doubt that the biological sciences, notably in their physiological aspects, are tending at the present time more and more to adopt a non-teleological point of view. From these points I again draw the conclusion that ours is a developmentally young science, that it still retains features of its early youth, and that the concept of purposeful adaptation is one of these features, sooner or later to be totally abandoned, even as the same concept has already been abandoned by the other natural sciences.

If my conclusion should be wrong, then one of two propositions must follow: either the sciences of the non-living have fallen into error, ought to have retained the concept of purpose in natural phenomena, and will sooner or later return to this concept; or else there is a great and fundamental difference between the living and the non-living, and teleology has a logical place in considerations of the former objects but not in those of the latter. Although it is to be realized that the possibility of one or the other of these propositions can not be rigidly denied at the present time, yet the probability of either one is definitely decreased by every analytical conquest of science. The controversy here suggested—which seems in our time as wastefully to absorb our energies as did the discussion of special creation in the time of Charles Darwin—is characterized by this peculiar feature, that, while all evidence presented *for* teleological causes is conspicuously based upon our ignorance and present inability to

analyze our problems, the evidence offered in the opposite direction is just as conspicuously positive and consists of cases which have already been subjected to relatively complete analysis. As Cowles[1] has pointed out, there has never been any retrogression in these matters; *all* phenomena now explained non-teleolgically were once explained teleologically, but no non-teleological explanation once attained, has ever been replaced by one involving purpose. Under these circumstances, a pragmatic judgment must be rendered, at least tentatively, in favor of the position here taken, that teleological thinking should have, and will at length have, no place in our science at all.

Conclusion.—I think it is to be concluded from the considerations here set forth that there is nothing known of the nature of living things which should lead the biological sciences to base their inquiries on any other methods or modes of thought than those employed in the sciences of the non-living. In both its aspects, passive and active, the dominance of the concept of adaptation, which now distinguishes our science from the non-biological ones, is related to the comparatively youthful stage of development so far attained by biology, and not to any observed character of the living objects with which we deal. It seems obvious that biology is advancing slowly but steadily along the path already traversed by the other natural sciences, and I think our present operations may best be guided by the hypothesis that all these sciences will eventually come to deal with the same fundamental concepts and modes of thought. Should this condition of affairs ever come to actual attainment, then the discussions which now center about the idea of adaptation might be expected to give place to other discussions of causal relations between measured qualities and properties of the objects dealt with, such as are already beginning to be common in many lines of biological study.

[1] Cowles, H. C., in Coulter, Barnes and Cowles, ''Text-book of Botany,'' 2: 948.   1911.

ADAPTATION IN ANIMAL REACTIONS[1]

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In recent times no feature of animal or plant life has been accorded greater emphasis than adaptation, and this property has been repeatedly declared to be one of the fundamental characteristics, if not the most fundamental, of living bodies. Nevertheless, the field of organic adaptation has been scarcely more than superficially surveyed. With the naïve instinct of the collector, the biologist has been content to roam over this vast territory and gather here and there what seemed to him to be striking examples of adaptation till our texts are rich storehouses of instances of nature's apparent ingenuity. How well founded even the more striking of these examples are, no one really knows, though the effect of the whole collection on the naturalist is to engender in him a feeling akin to awe for the adaptive capacity of living beings. May it not be, however, that we overestimate this aspect of organic nature and emphasize beyond reason its real value as a factor in the organic world? It is my opinion, at least, that many animal reactions which we have been accustomed to call adaptations should not be thus designated, and that the difficulties that we often meet in attempting to account for such reactions are due to our consideration of them from the standpoint of adaptations when in reality they are far from being such.

Adaptations are indissolubly connected with the activities of animals and plants. We are only just beginning to learn that an organism in its essentials is an active, working system, that the moment we think of it as

[1] Read at the Symposium on Adaptation at the meeting of the American Society of Naturalists, Cleveland, January 2, 1913.

a machine standing still, we divest it of precisely that
element which is most distinctive of it. The anatomical
conception of an organism as a mechanism at rest, useful
and important as it has been and is still, is thus funda-
mentally defective. The essential feature of every liv-
ing thing is incessant activity, and adaptations are part
and parcel of this activity. Even such apparently pas-
sive examples as the adaptation of a moth to the bark of
the tree on which it rests depends for success as much
on the position of the moth's body, the pose of its wings,
etc., all features of muscular action, as upon the color
pattern of the exposed parts. Thus adaptation, like
other truly organic phenomena, exhibits a fundamental
dependence on organic activity, a condition that favors
the conception of the organism as put forward long ago
by Lamarck.

But adaptation is not only essentially associated with
the activities of organisms; it is also conditioned by the
continuity of this activity. Every organic line of descent
has had its past history and can look forward to a pos-
sible future. The continuity thus indicated is an es-
sential part of organic nature. The inorganic may at
any moment be completely resolved into its elements and
recombined at the next moment into a new order without
violating the law of its existence. But an organism can
not undergo such a revolution without annihilation; an
animal or plant subjected to such a process would cea·e
to exist. Hence life is not only activity; it is activity so
directed as to be continuous, to be self-perpetuating.
Continuity of action is, therefore, an inherent part of
the make-up of living things, and adaptation is condi-
tioned by this continuity in that those reactions are
adaptive which make for a continuance of life.

Strictly speaking, adaptations exist no more in nature
than does a species; it is a word in the dictionary, a fig-
ment of the human brain. Just as the systematist finds
the individual animal or plant the real object of his in-
vestigation, so the student of adaptation finds individ-

ual animal movements the material for his study. Broadly speaking, these movements range from the hidden internal processes in the animal economy to the more obvious external forms of behavior.

The very fact that adaptations have been classed under one head to the exclusion of other forms of animal reactions has given them a certain undue prominence, but this is not the only reason for their usurping more than a fair share of attention. Many animal reactions that are in no proper sense adaptations have been brought under this head, and in certain quarters this process of appropriation has gone to such an extent that every animal reaction has been supposed to have some adaptive significance. How far this is from the truth can be made clear by a homely example. When a person faints, his best position for recovery is a horizontal one, and into approximately this position he is very likely to fall. Furthermore, he falls with limp muscles, a method which under the circumstances is much safer than that of falling with a tense body such as usually occurs in consciousness. Thus the position into which a fainting person falls and the method of arriving at it, have all the appearances of adaptations. Yet, in my opinion, any one who would interpret these movements as adaptations would lay himself open to a charge of unreality. The new position, favorable as it is for recovery, is in fact the mere consequence of the faint, and as such it completely loses any claim as an adaptation. That it is advantageous is purely incidental; it might equally well have been disadvantageous. Thus responses, even when of a favorable nature, are not necessarily adaptations, though they may resemble them to a striking degree. An adaptation is not only a favorable response, it is a favorable response especially developed to meet a particular emergency.

If it is so easy to point out pseudo-adaptations among our own activities, it is highly probable that they also occur among the responses of the lower animals. And

such seems to be the case. That an isolated blastomere representing a half or a quarter of the egg of *Amphioxus* should be able under favorable conditions to develop into a complete larva is at first sight a surprising fact and seems to give evidence of a remarkable power of adaptation. But such an interpretation is far from justifiable. The growth of the isolated blastomere seems to me much more like the falling of a fainting person than like a process devised to meet a special emergency, and, important and illuminating as this growth is from the standpoint of our understanding of the mechanism of the egg, it is, I believe, a good case of pseudo-adaptation rather than of true adaptiveness. All eggs certainly do not show this trait and to single out the egg of *Amphioxus* and extol this reaction as an adaptation is to give to it weight beyond its deserts. To call this an adaptation is to read adaptation into it as only an overzealous advocate could do. Dame Nature under the circumstances might well be likened to a certain English poet, who, on visiting incognito an exposition of his own verses, was amazed at the wonders they were said to contain.

The majority of animal reactions are, in all probability, neither conspicuously advantageous nor disadvantageous to the life of the individual. They are dependent chiefly on the material composition of the given organism, and, so long as they are relatively indifferent to the continuance of life, they pass without special consequence. Relatively speaking only now and then do we have conditions where a vitally important form of response, an adaptive response, appears. On the whole the flow of action in the daily life of many organisms requires little of such special activity and proceeds at the level of mild indifference. In other words, adaptive reactions as the controlling factors in animal life are, I believe, by no means so universal as some of their advocates would have us think.

The world at large affords an environment in which each animal has a wide range for possible reactions and

of a number of responses that might be made to a given
set of conditions, one may be quite as appropriate for
the continuance of life as another.   In other words ver-
satility seems to be a more truthful description of the
actual conditions in animal life than the rather rigid
state implied in the application of the idea of adaptive
responses.   Animal reactions in most cases seem to be
more of the nature of fluctuations than of mutations, to
borrow a related phraseology; they are individual idio-
syncracies that are insignificant so far as the race is con-
cerned and are usually not interfered with because of the
generous latitude permitted by the environment.   From
this standpoint animal reactions have a variety whose
explanation is to be sought for, as adaptations, but as an
expression of the momentary physical and chemical
make-up of the individual, a condition which does not
easily repeat itself and which therefore agrees with the
diversity of reactions exhibited by the organism.

Yet it is not for a moment to be assumed that adapta-
tions are not evident among animal reactions.   When it
is remembered what enormous numbers of young are
lost in the process of producing one adult and that much
of this loss is due to misdirected animal reactions, it is
impossible to believe that adaptations, as roughed out by
a crude selective process, should not have become in-
grained in most animals.   In fact any adequate survey of
the general field of animal reactions shows at once that
the main topographic features are adaptational and when
one reflects that this has probably been brought about in
large part by the elimination of myriads of individuals
mainly on the basis of some false step in their reactions,
one is compelled to admit that in our zeal for the study
of animal behavior, we may have missed the importance
of the lesson to be drawn from animal misbehavior.   But
however this may be, I am convinced that, though the
main reaction systems of animals are essentially adap-
tive, the details of their ordinary flow of responses is
mostly free from adaptive influence and proceeds on

lines determined chiefly by the momentary state of the individual concerned.

That animal reactions of an adaptive kind may possess qualities that apparently exceed the possibility of origin through selective operations has often been pointed out. In fact it is from this standpoint that adaptation as a sort of transcendental property of the organism has gained its most ardent votaries. And it must be admitted that the illustrations given in support of this view are most baffling and perplexing to the opponents. That a dog which has had its diet changed from bread to meat, should quickly exhibit a change in its pancreatic juice from a type well adapted to bread and poorly adapted to meat to another in which the reverse is true, is a fact of adaptation the explanation of which seems beyond reach. Here we are face to face with what appears to be a quick adaptation of a thoroughly successful kind and without the intervention of nervous activity. No wonder that in face of facts, such as these, the more speculative members of the biological camp seize their entelechies as the only weapons with which they may hope to do battle. But after all is the entelechy a reliable weapon. In all reactions of the kind just mentioned, we are prone to say that though there is not the least reason to suppose that intelligence has really intervened, the whole affair passes off as though directed by some such agent; hence we assume some intelligence-like factor, some entelechy, to be active for the time. But when we look at the matter deliberately, we must admit that intelligence is only our own expression for that aggregate of nervous states and actions which is our chief means of adaptation. To say then that one category of adaptive acts, the adjustment of secretions to particular kinds of food, has a fundamental resemblance to another category of adaptive acts, our intelligent performances, is not to offer an explanation but to leave the matter where it was. When we know more of the real nature of intelligence, we shall be in a better position to attack the problem of adaptive reactions, and,

conversely, when we know more about adaptive reactions, we shall be in a better position to attack the problem of intelligence. Meanwhile, do not let us deceive ourselves by confusing an argument in a circle with real progress. In attempting a solution of the problem of adaptive reactions, it is well to remember that entelechies and other like notions do not really bring us forward, for they are at most soporifics to the mind that would naturally be excited to research by precisely those questions that they tend to obscure.

In conclusion then I would maintain that the details of animal reactions are in the main free from adaptive restraint and that their diversity is dependent chiefly upon the fluctuating momentary condition of the animal body; further, that the main outlines of animal reactions are adaptive, but that when we attempt to explain this condition by assuming that it is dependent upon something like intelligence, we are arguing in a circle, for intelligence is merely our name for our own chief means of adaptation.

ADAPTATION FROM THE POINT OF VIEW OF THE PHYSIOLOGIST[1]

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I FEEL much ashamed in having to expose my intellectual nakedness before the members of this society. When I came to this meeting I supposed that adaptation, or the fitness of organisms to their environments, was a physiological truism; that fishes were fitted by their structures and functions to a life in the water; that frogs were so constituted that they could live either on land or in water; and I was even so ignorant as to believe that many structures of a bird's body adapted it to flight. But it appears from the paper of one of my colleagues that in all of these things I was most woefully mistaken.

I feel some hesitation, also, in appearing before a society composed largely of American students of genetics, for I have no new and confusing terminology to propose; and owing to my ignorance of the language they speak and of the short-hand symbols sometimes employed, I am, perforce, compelled to speak in ordinary English which may be understood by any one; all of which, I fear, must invest all I have to say with an air of superficiality, or even of simplicity. I am besides a confirmed conservative in the matter of evolution, holding fast to the explanation of adaptation given by Darwin of natural selection of small variations; having little or no confidence that genes, unit characters, mutations, saltations, allelomorphs, determiners, inhibitors, dominants and recessives, genotyes and phenotyes, are anything more than ghosts, without substance; and looking always for simple explanations of a physical and chemical kind, capable of

[1] Read at the Symposium on Adaptation at the meeting of the American Society of Naturalists, Cleveland, January 2, 1913.

expression in ordinary language, of the apparent complexities of evolution. I avow myself as a physiologist to be a follower of Darwin, admiring his methods of careful experiment and observation, his long cogitations, and with confidence in the soundness of his judgment. There has been a tendency of recent years in certain quarters to belittle his work, to make fun of his conclusions, to deny that evolution has been a slow and steady continuous process, as the rocks show, and to assert that it has taken place by a hop, skip and a jump, and that it would have taken place anyway without natural selection. Physics and chemistry have attempted to express the .physical world in terms of matter and energy, and many biologists are attempting to extend this method to the living world. While this is a necessary and admirable thing to do, it must not be forgotten that in doing so they are neglecting the main fact of life, consciousness, and that the phenomena of life can not be accounted for if this is neglected. It is obvious, too, that the physicist, with his present conception of matter and energy, is making as great a mistake in neglecting the psychical side of matter as the biologist would make if he neglected the physical side. For the psychical, like the physical, must be due to the properties of the atoms, or at least is associated always with them. For the atoms are the same in living and lifeless, their properties are inherent in them and can not be taken away and added to them as if they were wagons, which changed horses, as Du Bois Raymond has put it.

It is my opinion that physiology comes powerfully to the support of Darwin's conclusions; that it shows clearly that there are no such things as independently variable, unit characters; that a jump is a physiological impossibility; and that most so-called mutations are in reality reversions, as Darwin thought; and in this position physiology is, I believe, supported by paleontology.

But while accepting many of Darwin's conclusions, we must all admit that many phenomena are very hard

to understand on the basis of Darwin's explanations.
Among these difficulties, most of which were recognized
by Darwin, there are the phenomena of parallel evolu-
tion among different species and genera, which, though
diverse, appear all to be moving forward in the same
direction; the phenomena of steady, limited progress in
one direction which point toward orthogenetic variation;
the phenomena of the appearance of rudiments and their
development until useful. It is exactly these difficulties
upon which physiology throws some light; and it is of
them that I particularly wish to speak.

In the evolution of animals two movements may be
perceived: a spreading out and a progress; a diversifica-
tion and a movement forward. The first movement is
illustrated by the formation of many different species
in one genus; or of many genera of the same type of
animal; the second by the movement forward in the line
of evolution of all these species. These two movements
were not sharply distinguished by Darwin, but they have
been more or less clearly recognized by several philoso-
phers. It is this double movement which has given the
animal kingdom the form of a branching tree instead of
a single trunk. Darwin dealt mainly with the first of
these movements, which gives rise to genera, species and
varieties; which is shown by the diversification of ani-
mals and plants in domestication by human selection;
and he explained it by the progressively better adaptation
of forms to particular environments. He believed the
second movement, the movement upward, was due to the
same cause.

It is the second movement which has been so hard to
explain and which has particularly puzzled the paleon-
tologist; the successive series of dominating types on
the earth's surface culminating in man; the progress
steadily toward the goal of consciousness and intelligence.

The question which I wish to raise is whether these two
movements, which are at right angles to each other, may
not be due to the natural selection of two different kinds

of adaptations: first, adaptations of form and function to different kinds of environments; and second, the natural selection of the function of irritability, or, in other words, to the selection of adaptability, or the adaptation to changeableness of environment. Selection of the first kind of adaptations may have given rise to varieties, species, genera of the same type of animal, and have produced the spreading, or diversification; while selection of the second kind of adaptation may have produced the movement onward and upward of all animal forms.

These two kinds of adaptations do not always go together and selection of the one may outweigh the other. It is because selection to a specific environment sometimes is more important than selection of adaptations to changeableness, that not all organisms have progressed in the scale of evolution equally rapidly: but some have persisted in special environments with slight changes of structure for very long periods, or may even have retrogressed; while other forms, in which the second adaptation has been rigorously selected, have moved rapidly onward and upward, and show little adaptation to any special environment.

The question whether evolutionary progress is due to the selection of this second adaptation, that of adaptability, occurs very naturally to a physiologist, because, in the first place, the evolutionary development of consciousness and intelligence appears to him to be one of the most important, if not the most characteristic movement in evolution; and in the second place, his point of view in considering evolution and adaptation is somewhat different from that of the zoologist or the paleontologist. To him the organism does not appear constituted of bones, skin, horns, or other structures, but to be constituted essentially of a number of mechanisms in activity, each mechanism having a definite function to perform. Evolution, for the physiologist, is not evolution of structure primarily, but evolution of function; and he natu-

rally expects to find that the adaptations of function have been of great importance in determining survival.

Of all the physiological properties of the original protoplasm upon which natural selection might be supposed to act, irritability, the most fundamental property of living matter, would seem the most probable point of attack; for irritability is that property of protoplasm in virtue of which it adjusts itself to its environment. It is the property of response; and since it is the environment which is acting as the judge of the excellence of the response and doing the selecting, it would seem that it must be upon this property that all organisms must be tested. It is, moreover, this property that Spencer has very acutely selected as the most fundamental characteristic of living organisms, namely, the power of continuous adjustment of internal to external conditions. It would seem probable that however well animals might be adapted to special environments by the action of natural selection, this particular property, or function, which has to do with the continuous adjustment of internal to external relations must have been throughout the whole course of evolution of predominant importance. And if there has been any unity in the progress; if the course of evolution has been at all in any single direction; and if the natural selection theory is true; it must be in the direction of the perfecting of this function.

I think this short statement will make it clear why the physiologist turns naturally to this fundamental quality, or property of living things, when he considers evolution and adaptation; for however organisms may vary in structure or other particulars, they all have irritability in common. Moreover, I think most physiologists will agree with me that this particular property has been too often neglected by most students of evolution, among whom physiologists have been unfortunately very rare.

Irritability shows itself in all cells by the power of internal change in response to an external change. In most cells of the body there is nothing especially adaptive

in the nature of many of these responses; but it is quite
otherwise, if we consider the organisms as wholes.   It
is clear that all organisms have not only the power of
reacting to an external change, but many of their reac-
tions are adaptive to a surprising degree.   This is indeed
the very crux of the difference between living organisms
and lifeless things.   A lifeless thing can not adjust its
internal to its external relations so that it can continue
to exist in a changed environment.   A crystal in a solu-
tion of its kind must dissolve, if the concentration is kept
ever so little below saturation; a whole universe must
pass away, if anywhere within it there is a persistent
uncompensated difference of potential. With living things
it is quite otherwise. They have the power of interposing
resistances to the potential difference. All living things
without exception have adaptive responses so that they
are able to continue in existence even though their sur-
roundings change in many different ways. They possess
adaptability.   Their responses due to their irritability
are adaptive responses. The irritability of the organism
as a whole is, then, above everything else characterized
by power of adaptive response.

It is not difficult to imagine how this specialization of
the general property of irritability arose. Some of the
indefinite responses of the original organisms to environ-
mental change protected the organism against the change.
Organisms with such responses survived and their de-
scendants had the property of a limited adaptive response
to this particular change. From this crude beginning
further progress was easy. The changes in the environ-
ment, though many, are not indefinite in number, and
adaptations in the nature of direct responses easily arose
and were perfected.

Adaptability, then, appears to the physiologist as the
master word of evolution. And many facts also may be
urged as confirming this conclusion. For example, one
and all of the great physiological mechanisms of the body
have a single purpose: to secure adaptability.   Not to

adapt an organism to one environment, but to all environments, and thus to make it superior to all environments. Furthermore, the higher organisms are specially remarkable for the development of that master tissue of the body which is preeminently irritable and of which the main function is the adjustment of internal to external relations, the nervous system; and finally that the inference is sound may be concluded from the fact that it is by adaptability and by no other quality whatever that organisms may be arranged in the order of their evolutionary progress.

It is not at all surprising that adaptability should be the most important adaptation in nature, overpowering, except in special cases, and dominating all others. For there is but one certain thing in nature: namely uncertainty. The most constant feature of all environments, but particularly of land environments, has been their inconstancy. Changeableness is the chief characteristic of all environments, whatever their special characters may be. There are changes of light, temperature, climate, oxygen and carbon dioxide, moisture; changes due to the introduction of new species by migration upsetting nature's balance; changes in the food supply. Climates, flora and fauna change; change alone persists. Change is the essential thing. We may expect, therefore, if Darwin be correct in his conclusion that variation and natural selection account for evolution, that adaptation to changeableness must be the chief adaptation in nature, and more than all others, it must have determined the general course of evolution. This is found to be the case and the great physiological mechanisms of the body are designed, as already stated, to subserve this fundamental adaptation. Adaptability is that power which fits organisms to withstand the unexpected: the vicissitudes of life; special adaptations of form and color may contribute to the survival of animals; but the essential, or root, adaptation is to changeableness. By adaptation to all environments they become finally superior to all environments.

Superiority to environment, and not adaptation to it, is secured through the irritability of the organism considered as a whole.

The great mechanisms of the body which have this function are several. First, the heat-regulating mechanism, for by means of this organisms are rendered independent of the temperature of their environments. They can exist in the tropics or in the arctics and withstand the extremes of our own climate, while maintaining their activities. This is a complex mechanism consisting of insulating material in the skin; trophic nerves to the internal organs; a closed vascular system; a power of rapid oxidation; supra-renal capsules; pancreas; nervous coordination; sweat glands; evaporation of water in the lungs; temperature nerves. More than any other this mechanism enabled the mammals to conquer the reptiles and supplant them. The mammals became independent of the temperature of their environments. A mechanism not coming by jumps, but the rudiments found far down in the fishes and slowly evolved.

A second fundamental mechanism of great importance for the mammals in supplanting the reptiles and other animals probably was that concerned in immunity. Most of the toxins of poisonous reptiles are of a protein nature. The mammals have developed a mechanism, the details of which are still obscure, but which apparently consists in the conversion of these protein toxins into bodies which neutralize the toxins from which they are formed, that is, into antitoxins. We find, as a matter of fact, that at least many of the mammals are able apparently to make an anti-toxin out of any kind of a foreign protein. Besides this mechanism of defense, useful against bacteria, as well as against snakes, there is the primitive mode of phagocytosis and the chemical method of defense, which consists either in the prevention of absorption, or in the chemical neutralization of the poison by union with other substances. Thus the toxicity of phenols, benzoic acid and many alkaloids are neutralized. By this mechanism

mammals are rendered superior to the attacks of many of their enemies and to this extent rendered superior to their environments.

Third, there is the mechanism for rendering mammals tolerably independent of the moisture content of their environment, a mechanism most highly developed in the reptiles. A mechanism formed by the replacing of the wet skin of the amphibian by a dry or scaly skin; the perfecting of the kidneys to maintain osmotic pressure of the blood; the control of the sweat glands and loss of water by the intestines; the development of membranes non-permeable to salts, so that animals may sit in fresh water and not lose their salts. One of the most interesting parts of this mechanism is shown in the reptiles and birds, in the substitution of uric acid for urea in their excretions. By this improvement reptiles have secured almost complete independence of the water content of their environments. They make enough water in their own bodies to supply their small losses. This again is a mechanism of which we can trace the steady growth without a break from the invertebrates to man.

A fourth great mechanism makes mammals independent of barometric fluctuations and less dependent on a fixed atmosphere. By means of their blood loaded with hemoglobin carried in corpuscles lacking all oxygen-consuming power, they are able to live on lofty plateaus, or in deep valleys; and in the presence of much or little carbon dioxide.

The mechanisms having to do with reproduction and the caring for the young afterward have this same advantage of rendering the mammals independent of environment.

A sixth mechanism is the alimentary mechanism, most highly perfected in man. This has rendered him independent of any particular kind of food. He can make his body of any kind of plant or animal. He can make carbohydrate out of protein and many other things. He can live in any climate largely because of this mechanism.

Again a complex mechanism, consisting of teeth, of digestive glands tearing proteins and carbohydrates to pieces, so that he can build up his own proteins from any other kind, useless amino acids being converted into sugar and urea.

The last and by far the most important of these great mechanisms of adaptability is that which provides for every contingency; for the unexpected. It seems that nature, after elaborating these other mechanisms to meet particular vicissitudes, has lumped all other vicissitudes into one and made a means of meeting them all. One can not but be pleased by the apparent ingenuity of this solution. I refer to the nervous mechanism. It is obvious how this mechanism, by substituting choice for blind instinct, consciousness for unconsciousness, developing memory, so that one can profit by experience, and intelligent adaptation of means to ends, has provided finally for all possible contingencies of the future. She has spoken her last word. Adaptability, or superiority to environment, was the end so blindly sought; memory, consciousness, choice were the means, shall I say the means as blindly adopted?

To the physiologist, then, adaptability appears to be the touchstone with which nature has tested each kind of organism evolved; it has been the yard stick, with which she has measured each animal type; it has been the counterweight against which she has balanced each of her productions. However well adapted to a specific environment a type might be, did it lack ever so little of its possibilities in this direction, it was sooner or later relegated to the scrap heap. Some forms, to be sure, persisted in special environments, where they were protected from competition, as in Australia; or where the environment was fairly constant, as in the sea; or in special environments for which they were highly suited; but the whole trend of evolution, with these exceptions, may be summed up by the statement: the general course of evolution has been always from the beginning to the end, in the direc-

tion of increasing adaptability or increasing perfection of irritability. This law may be put by the side of the law for the evolution of universes: all spontaneous change is in the direction of increasing entropy.

It is not by form, by color, by increasing complexity or simplicity, that animals may be classified in the order of their evolutionary appearance. It is by this property of adaptability and this alone. At the summit is man; now consciously attempting to carry on what nature has been unconsciously attempting these millions of years, and to secure mastery of his environment. Below him are the other placental mammals of lower intelligence; beneath them the marsupials, less adaptable than the mammals, because of lower brain power; then the reptiles independent of water, but not of temperature; the amphibia, only partially independent of water, but not of temperature; the teleosts able to live in salt and fresh water; the selachians, most without osmotic control and limited to the sea; the arthropods living on land and sea, but dependent on temperature, food and climate, cramped by an external skeleton, and with the fatal defect of running the alimentary canal through the nervous system, so that for higher brain power, either a new nervous system or a new alimentary canal would be needed; lower still the molluscs and annelids, closely limited to their environments; and last the echinoderms and protozoa. No adaptation or power of the body has been so consistently attacked by natural selection as this; and it is this property which seems to have been the determining factor in the general course of evolution and to have determined the steady development of the psychic powers.

I come now to the second part of my subject, namely, correlation. By the first part I have attempted to show that the selection of variations in adaptability is responsible for at least a part of the steady progress in one direction of many kinds of animals; and explains that unity of progress which has been one of the main causes for assuming orthogenesis. In this second part of the

paper, I hope to show that the development of our knowledge of correlation removes some other difficulties which Darwin had to meet, and probably explains some other facts which have been urged as supporting orthogenesis.

Among the puzzles of evolution has been the steady growth of rudimentary structures which have apparently no function until they are considerably developed. I say *apparently* no function, for the physiologist has learned to be very cautious in saying that any part of the body is without function or use. A few years ago it was quite otherwise and it was supposed that various rudiments, like the appendix, the hypophysis, the pineal gland, the thymus and some other organs were without function; the surgeons were busy explaining how much better we were off without them; and the anti-Darwinian was fond of presenting these things as not consonant with the view of adaptation. At the present time the uselessness of these rudimentary structures is no longer affirmed. We must therefore be very cautious in supposing that any structure we see, no matter how insignificant it may appear, is without importance. Darwin himself felt the great fact of correlation, and his pangene theory was invented, in part, to account for these facts. He would be both astonished and delighted could he know how completely physiology has vindicated his appeal to correlation as the explanation of some difficulties.

Modern physiology has shown that the whole animal organism is correlated by means of internal secretions; that there' is but one unit in the body, and that is the whole organism. By the work of Knowlton and Starling we now have the final proof of the correlation of the pancreas and muscles. The correlations between the hard and soft parts of the body are of still greater importance to the paleontologist, for it has been shown that the hard parts are not independently variable, but that they are dependent at every point upon the function of the soft, internal organs. Who would have dreamed that the character of the skin, the hair, the shape of the skull, the in-

telligence itself, the length of the limbs, or the speed of transformation of a tadpole into a frog would be dependent on the thyroid or thymus gland? That the minute parathyroids should be absolutely necessary to the life of an organism thousands of times their weight? Or that the development of the testes, the change of milk teeth to the permanent dentition, the growth of the bones of the extremities, should be dependent on the anterior lobe of that apparently useless rudiment, the hypophysis? Or that the secretion of milk and urine should depend on the posterior lobe of the same organ? Who had the temerity to suggest that the corpus luteum should be influencing the development of the mammary glands? Do we not see, indeed, that most of the characters of the body which have steadily developed from the fishes to man are secondary characters dependent on the anterior development of these ductless glands? Is this fact without significance to the paleontologist in helping him to understand the apparent steady progress in one direction, the appearance of orthogenesis? It will be asked, perhaps, what has caused the steady development of these glands. But the answer is not difficult. They are, in their turn, parts of the mechanism of adaptability which has been consistently selected in evolution. They are concerned not only in the growth of bone, but in the growth of the nervous system, the heat control of the body, the immunity mechanisms, the efficiency of muscles, and are in the chain of reproduction itself. These facts largely remove, in my opinion, the difficulties in understanding how rudimentary organs could be useful.

But not only do these facts remove these difficulties in the way of the selection theory, but they have a no less important bearing on the problem of heredity. They show that there can be no independently variable qualities in the animal body. The body is a unit, and I, at least, can imagine no part of it which can vary without influencing other parts. Correlations are everywhere. Pigment is often cited as a unit character, but how can it

be so? Pigment is itself the result of a long and complex
series of changes. If a given cell produces no pigment it
is perfectly certain that its other chemical processes
are to some degree modified also, so that these other
things vary also. If this cell is changed so that it pro-
duces no pigment, then since it is the logical result of a
long series of changes in the developing organism, those
changes must have been different in animals producing
pigment and no pigment. But this means, since each
process in the early stage of development influences a
multitude of processes in the final change, that there must
be a host of differences correlated with the pigment
change. As a matter of fact, Darwin long ago pointed out
that pigment production was apparently correlated with
other factors; particularly with vital resistance, a fact
repeatedly mentioned to the writer, also by Whitman as
a result of his experiments in pigeon breeding. Darwin
cites the case of the Virginia pigs of which only the black
ones could eat a poisonous root without losing their hoofs;
and Whitman told me that always birds deficient in pig-
ment were also somewhat deficient in other characters
and were weaker.

The essential unity of the organism is not only fatal to
the whole theory of unit characters, but it is an insuper-
able objection to the theory that evolution has been by
jumps. The organism is a finely adjusted mechanism of
a very complex kind; it seems impossible to a physiolo-
gist that one can cause a sudden large change in any part
of it and have it continue to function; it is as incredible
as if one should remove one of the wheels of a watch,
replace it by a larger one, and expect the watch to con-
tinue to run. Such a simple matter as the replacement
of urea by uric acid as an excretion, a change which the
reptiles introduced in their differentiation from the am-
phibia, a change which might conceivably be brought
about by the dropping out of a uricolytic enzyme, could
not take place suddenly. The kidneys and all other organs
of the body would need to be adjusted to this change.

Finally correlation has greatly enhanced the value of the old idea of checks in development and shows most clearly that no organ of the body ever reaches its full potentialities. What comes out of an egg is but one of the infinite potentialities contained in it. Velocity of development, like every other chemical reaction, is equal to the affinity divided by the resistance. If resistances are increased, or if vitality, in other words chemical affinity, be reduced, the development must stop sooner than normal; and we have the phenomena of reversion. If, on the other hand, the reverse takes place, if vitality is increased or resistance reduced, we have variation in the direction of evolution. The development of nonviable monsters is at one extreme of this process. Ontogeny is like a runner, taking the first hurdles easily, but always with increasing difficulty, sometimes trippling at one, sometimes at another, but never reaching the end of his race.

In conclusion then: to the physiologist it appears that the best explanation of adaptation is that given by Darwin of natural selection of small variations; that the essential unity of the progress in evolution toward consciousness and intelligence has been due to the natural selection of the fundamental property of irritability, for it is in virtue of this property that adaptability of organisms has been increased. The recognition of this fact removes one of the difficulties in the way of Darwin's theory. And, second, physiology by the establishment of the physiological correlation of all parts of the body, hard and soft, interposes a final objection, in my opinion, to the whole theory of unit characters, of independent variability of characters, and to the theory of evolution in any other way than by a slow and gradual process, which shall give time to the readjustments of every part of the body necessitated by a change, however slight, in any part of it.

THE FITNESS OF THE ENVIRONMENT, AN IN-QUIRY INTO THE BIOLOGICAL SIGNIFI-CANCE OF THE PROPERTIES OF MATTER[1]

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Darwinian fitness is compounded of a mutual relationship between the organism and the environment. Of this, fitness of environment is quite as essential a component as the fitness which arises in the process of organic evolution; and in fundamental characteristics the actual environment is the fittest possible abode of life. Such is the thesis which I seek to establish. This is not a novel hypothesis. In rudimentary form it has already a long history behind it, and it was familiar doctrine in the early nineteenth century. It presents itself anew as a result of the recent growth of the science of physical chemistry.

In the study of fitness it has been the habit of biologists since Darwin to consider only the adaptations of the living organism to the environment. For them in fact the environment, in its past, present, and future, has been an independent variable, and it has not entered into any of the modern speculations to consider if by chance the material universe also may be subjected to laws which are in the largest sense important in organic evolution. Yet fitness there must be, in environment as well as in the organism. How, for example, could man adapt his civilization to water power if no water power existed within his reach?

At first sight it may well seem that inquiry into such

[1] Read at the Symposium on Adaptation at the meeting of the American Society of Naturalists, Cleveland, January 2, 1913.

[1] This paper consists chiefly of excerpts from a book of the same title soon to be published by the Macmillan Company.

a problem must end unsuccessfully in vague and unprofitable guesses. But the physico-chemical basis of life it at length firmly established. On the whole, the composition of living matter, its physical structure, the changes of matter and energy which constitute the metabolic process, together with the totality of such changes, which make up the fundamental economic process of that largest community which consists of all living beings, are all clearly defined.

The Characteristics of Life

Under these circumstances it is certainly no rash enterprise to seek a definition of some of the essential characteristics of life. Although it is probably far beyond our present power to make a complete study of the problem, I feel sure that a brief analysis will justify certain very definite conclusions. Life as we know it is a physico-chemical mechanism, and it is probably inconceivable that it should be otherwise. As such it possesses, and, we may well conclude, must ever possess, a high degree of complexity—physically, chemically and physiologically, that is to say, structurally and functionally. We can not imagine life which is no more complex than a sphere, or salt, or the fall of rain, and, as we know it, it is in fact a very great deal more complex than such simple things. Next, living things, still more the community of living things, are durable. But complexity and durability of mechanism are only possible if internal and external conditions are stable. Hence automatic regulations of the environment and the possibility of regulation of conditions within the organism are essential to life. It is not possible to specify a large number of conditions which must be regulated, but certain it is from our present experience that at least rough regulation of temperature, pressure, and chemical constitution of environment and organism are really essential to life, and that there is great advantage in many other regulations and in finer regulations. Finally a living being must be active, hence its metabolism must be fed with matter and energy, and

accordingly there must always be exchange of matter and energy with the environment.

Obviously these few conclusions can make no claim to completeness. Fully to describe life, the discovery of many other fundamental characteristics is necessary, including such as are related to inheritance, variation, evolution, consciousness and a host of other things. But in the formation and logical development of such ideas there is danger of fallacy at every step, and, since the present list will suffice for the present purpose, further considerations of this sort are best dispensed with. This subject should not be put aside, however, without clear emphasis that the postulates which have been adopted above are extremely meager. The only motives for abandoning further search are the economy and the security which are thereby insured and the very great difficulty of extending the list.

The Environment

Even at the earliest period in the evolution of a typical star there appears to be a progressive variation in the chemical composition from center to periphery. Theoretically it seems inevitable that the heaviest elements should be concentrated in the interior and that those of lowest atomic weight should be present in the greatest amount near the surface. Actually, spectroscopic investigation fully confirms this view. Thus the spectra of typical hot stars show that hydrogen is an inevitable constituent of their superficial parts. Indeed the universal presence of hydrogen under such circumstances is undoubtedly one of the most clearly established facts of stellar astronomy. As stars cool and become red the spectral changes quite as unmistakably point to the presence of carbon. Accordingly we possess the best of evidence and the best of reasons for the belief that large quantities of hydrogen and carbon must exist at or near the surface when a crust forms upon a cooling star.

The nature of the chemical combinations into which these elements at first enter is perhaps open to some

question. But as the temperature falls in the cooling of a sun or planet the affinities of carbon and hydrogen for oxygen increase so that carbonic acid and water must normally result. For oxygen is almost certainly present in the sun, it is found in meteorites, and the vast store of it in the earth's atmosphere and crust (roughly one half of their total mass) justify the belief that it is everywhere one of the commonest of elements. Hence an atmosphere containing water and carbonic acid appears to be a normal envelope of a new crust upon a cooling body. Even were not these substances at first present in such an atmosphere, volcanos must soon belch them forth in enormous quantities, to relieve the pressure which inevitable chemical processes set up.

In short just as living things permit themselves to be simplified into mechanisms which are complex, regulated, and provided with a metabolism the environment may be reduced to water and carbonic acid. These are simplifications counselled solely by expediency. Neither logical process is necessary, each involves a disregard for many circumstances which might be of weight in the present inquiry. But in the end there stands out a perfectly simple problem which is undoubtedly soluble. That problem may be stated as follows: In what degree are the physical, chemical, and general meteorological characteristics of water and carbon dioxide, *the primary constituents of the environment* and of the compounds of carbon, hydrogen and oxygen favorable to a mechanism which must be physically, chemically, and physiologically complex, which must be itself well regulated in a stable environment, and which must carry on an active exchange of matter and energy with that environment.

The first step in seeking a solution must be to review the data of physics and chemistry which describe the properties of water and carbonic acid, having due regard to their meteorological significance. Such data of the highest accuracy exist in great profusion, for almost every conceivable property of these substances has been

studied with patient care. Next, the properties of the compounds of carbon, hydrogen, and oxygen must be considered, and some of the characteristics of the chemical reactions into which they enter must be discussed. For this examination the unparalleled development of the science of organic chemistry provides ample material. All of these things must be scrutinized quantitatively as well as qualitatively, and again there is no lack of necessary formation.

Immediately one advantage of the method here proposed becomes evident. We can deal with the familiar abstractions of physical science—specific heat, coefficient of expansion, solubility, heat of reaction, etc.—and thereby we shall gain all the advantages of the most exact sciences. No qualifications, no doubtful or contentious matter, no imperfect descriptions need enter.

In this manner it will be easy to estimate the absolute biological fitness in certain respects of water and carbonic acid, and at once a host of automatic results of their properties will become evident. Many of these results, such as the nearly constant temperature of the ocean, the ample rainfall, the freezing of water upon the surface, the great variety of carbon compounds, are familiar subjects of speculation, though since Darwin little interest has been manifested in them; others, only recently brought to light by the growth of physical science, are nearly or quite unknown in this connection. All deserve to receive more serious attention from biologists than is at present vouchsafed them, for they constitute a part of the very foundation of general biology, and they cause many of the phenomena with which man is concerned in his struggle for mastery of the environment.

Yet the mere exposition of such facts and relationships can not suffice in a discussion of the fitness of the environment. In the first place these are in the main familiar ideas, and if they were altogether conclusive to prove the existence of really significant fitness, if they could be regarded as alone adequate to establish the necessity of

putting fitness by the side of adaptation as a coordinate factor in causing the marvels of life, it is hard to believe that they would have been so long neglected. In the second place there is nothing comparative about such information. Water is indeed a wonderful substance which fills its place in nature most satisfactorily, but would not another substance do as well? Is not ammonia, for example, a possible substitute? And are there not many other chemical bodies which might, in a very different world, serve equally useful purposes? Perhaps, too, the great variety of carbon compunds which are known to the chemist are known only because the vital processes furnish an abundance of material with which to experiment. Is it not possible, therefore, that another element, perhaps for instance silicon, may enter into even greater varieties of compounds? It is such questions, ever present in the minds of men of science yet never yet carefully scrutinized to see if an answer be possible, which, I suspect, have long deflected attention from this subject.

Clearly, therefore, it will be necessary to compare the properties of water and carbonic acid and of the carbon compounds with those of other substances. It will be necessary to find out whether these substances are not only fit but fittest—and this no doubt is a task of a very different sort. It may even seem, at first sight, an impossible one, but I hope to show that this is not the case, and that in spite of the incompleteness of our physical and chemical knowledge, it may be pressed to a satisfactory issue.

The very constant temperature of the ocean is a most important factor in the economy of nature. It constitutes, for example, a vital regulation of the environment of a large proportion of all the living organisms of the world, and it has many other important "functions." This constancy of temperature is in large part due to the magnitude of the specific heat of water. Other things being equal the greater the specific heat of water the more constant must be the temperature of the ocean. If then

the specific heat of water, as is actually the case, be nearly or quite a maximum among all specific heats, it follows that the fitness of water in this respect is nearly maximal.

Again the ocean contains an astonishing variety of substances in solution, and they are present often in large quantities. In this manner a very great supply of food in very great variety is offered marine organisms. Of course such richness of the environment is an exceedingly favorable circumstance for the organism, and it is due principally to the ability of water to dissolve a multitude of things in large quantities. It is not to be supposed that the substances present in sea water are all of use to every organism. This need not be the case at all, but a variety of supplies which may be adapted to special requirements as they arise, here iodine, there copper, for instance, is a very genuine advantage. Further the vast utility of the solvent action of water in blood, lymph, and all the body fluids is too patent to call for comment. If, now, it can be shown that the solvent power of water is nearly or quite a maximum, as it really is, among all known solvents, then it must be evident that in another respect the fitness of water is nearly or quite maximal.

Again the amount of energy that is required to tear apart molecules of water and liberate hydrogen and oxygen is very great indeed, and when hydrogen and oxygen recombine to form water this energy must reappear,— under ordinary circumstances as heat. This fact too is very favorable for the organism, because almost all compounds which contain hydrogen yield a great deal of energy which can be tapped in the process of metabolism. If therefore the heat of combustion of hydrogen be nearly or quite a maximum, as it is, among all substances, it is clear that water is again, in another respect, most wonderfully fitted for life. Finally, if it be true, and such is the case, that very few of the substances which share the fitness of water in one of these characteristics, also share or approach its fitness in either of the others, and that none possesses all these qualifications in a degree that merits consideration, it must, I conceive, be ad-

mitted that so far as the investigation has proceeded, water is the only possible fit substance.

A criticism may here be made, are there not other substances which possess other groups of qualifications which water lacks? And that is a difficulty which is even harder to meet. But in the first place it is evident that there are not an infinity of important physical properties; in fact there are very few. And in the second place it is evident, both from centuries of experience in physical science and from the postulates above mentioned regarding life, which undoubtedly do in the main describe its physico-chemical characteristics, that very few properties indeed are of importance in the least comparable with those which I have mentioned. Finally it is in the highest degree probable that we are acquainted with most of the truly essential physical properties, and know them as biologically important, when they are so; and I believe it has been possible to consider them all, and thus make the argument complete.

Such is the nature of the argument; the facts, though no less important than those above indicated, are far too numerous to mention. They include the unique surface tension of water and its very great ionizing power, the absorption coefficient and ionization constant of carbonic acid, the extreme chemical activity of oxygen and hydrogen, the unique chemical combining power of carbon, the number, complexity, variety and chemical activity of the compounds and processes of organic chemistry, and the vast complexity of the chemical system which inevitably results from the reduction of a mixture of carbonic acid and water. These properties result directly in a bewildering variety of conditions which in the most varied ways promote complexity, durability and metabolism.

Analysis of all the facts justifies the following conclusions.

The physical and chemical properties which have been taken into consideration include nearly all those which are known to be of biological importance or which ap-

pear to be related to complexity, regulation and metabolism.

There are no other compounds which share more than a small part of the qualities of fitness of water and carbonic acid, no other elements which share those of carbon, hydrogen and oxygen.

None of the characteristics of these substances are known to be unfit, or seriously inferior to the same characteristics in any other substance.

Therefore the fitness of the environment is both real and unique.

In drawing this final conclusion I mean to assert the following propositions:

I. The fitness of the environment is one part of a reciprocal relationship of which the fitness of the organism is the other. This relationship is completely and perfectly reciprocal; the one fitness is not less important than the other, nor less invariably a constituent of a particular case of biological fitness; it is not less frequently evident in the characteristics of water, carbonic acid and the compounds of carbon, hydrogen and oxygen than is fitness from adaptation in the characteristics of the organism.

II. The fitness of the environment results from characteristics which constitute a series of maxima—unique or nearly unique properties of water, carbonic acid, the compounds of carbon, hydrogen and oxygen and the ocean—so numerous, so varied, so nearly complete among all things which are concerned in the problem that together they form certainly the greatest possible fitness. No other environment consisting of primary constituents made up of other known elements, or lacking water and carbonic acid, could possess a like number of fit characteristics or such highly fit characteristics, or in any manner such great fitness to promote complexity, durability and active metabolism in the organic mechanism which we call life.

It must not be forgotten that the possibility of such conclusions depends upon the universal character of

physics and chemistry. Out of the properties of universal matter and the characteristics of universal energy has arisen mechanism as the expression of physico-chemical activity and the instrument of physico-chemical performance. Given matter, energy and the resulting necessity that life shall be a mechanism, then the conclusion follows that the atmosphere of solid astronomical bodies does actually provide the best of all possible environments for life.

<div align="center">Vitalism</div>

Modern vitalism consists in asserting the existence of a directive tendency which manifests itself in or through the organism alone and is peculiar to life.

In such speculations the properties of matter and the processes of cosmic evolution have no place. Bergson indeed very definitely, and it would seem gratuitously, puts aside cosmic evolution, and also with slight reservations the properties of matter, as of no essential consequence in organic evolution.

Yet whoever is disposed to speculate about biological fitness, and not even the incomparable finesse of M. Bergson's dialectic can make fitness other than the most general result of the process of organic evolution, must now weigh well the cosmic processes. For, if allowance be made for the results of natural selection, fitness of environment has the greater claim to be considered.

The two fitnesses are complementary; are they then single or dual in origin? The simpler view would be to imagine one common impetus operating upon all matter, inorganic and organic, through all stages of its evolution, in all its states and forms and leading to worlds like our own through paths apparently purposeful. Such it seems to me is the natural hypothesis for the vitalist to adopt. But then vitalism vanishes, only teleology remains. Yet putting aside mechanistic differences is it not now lost in any case? Has not modern vitalism in accepting the limitation to entelechies or impetus destroyed itself?

The situation, briefly, seems to be as follows: Two evo-

lutionary processes independently result in two comple-
mentary fitnesses, hence they are related. In the one
process the origin of fitness is in part explained by a
mechanistic hypothesis. Nevertheless many philos-
ophers, as is their right, declare that in this process a
further extra-physical influence is to be assumed. But
any one who makes such an assumption for the one proc-
ess must certainly make it for the other, thus he will be
led to see impetus or entelechies everywhere. Under
these circumstances it may be doubted if his acquaintance
with the nature of his impetus or entelechies is so inti-
mate that he will be able to distinguish the inorganic
from the organic, for he has surrendered all positive
physico-chemical differences between organic and inor-
ganic bodies and processes to the mechanist. Hence,
unless he is to make an arbitrary and unintelligible dis-
tinction, or to indulge in the spinning of cobwebs, his
vitalism has ceased to be exclusively organic, in short,
has ceased to be vitalism at all, and has become mere
universal teleology.

The whole process of cosmic evolution from its earli-
est conceivable state to the present is, however, pure
mechanism, as the most perfect induction of physical
science, based upon each and all of its manifold suc-
cesses in accounting for the phenomena of nature con-
clusively proves.

But if cosmic evolution be purely mechanistic and yet
issue in fitness why not organic evolution as well? Thus
once more we arrive, this time more completely, at the
negation of vitalism. Mechanism is enough in physical
science, which no less than biological science appears to
manifest teleology; it must, therefore, suffice in biology.
We possess two arguments; the argument that, except
mechanistically, organic and inorganic phenomena are,
in such aspects as concern physical science, alike, and,
therefore, a specifically vital teleology is unnecessary,
and the argument that inorganic science unquestionably
has no need of non-mechanistic teleology. Hence we
are obliged to conclude that metaphysical teleology is to
be banished from the whole domain of natural science.

SHORTER ARTICLES AND DISCUSSION

MUTATIONS IN ŒNOTHERA BIENNIS L. ?

It is evident that the adherents of the mutation theory are sensitive to the doubts freely expressed concerning the status of *Œnothera Lamarckiana*, the behavior of which in throwing off marked variants is cited as the most important evidence for the origin of species by mutations. These doubts are in fact criticisms of the assumption that *Lamarckiana* is representative of a wild species and express the view that this plant is of hybrid origin and that its behavior is of the sort to be expected of a hybrid. Consequently, mutationists are likely to bring forward as rapidly as possible any evidence that may seem to indicate the appearance of clear inheritable variations of a marked character in forms of pure germinal constitution, *i. e.*, in homozygous material.

There are types of *Œnothera* that we have reason to believe are now very pure and have been so for a great many years. Such a form is the *biennis* of the sand dunes of Holland. This species has apparently been established in its habitats in Holland since pre-Linnean times. There has been little opportunity for chance hybridization and its habits of close or self pollination in the bud are greatly in favor of the continuation of its germ plasm in pure lines. Moreover, the type in experimental cultures of De Vries and others has proved to be constant. If then it could be shown that tested strains of this *biennis* are able to produce new forms of specific rank or even marked varieties the mutationists would have much stronger evidence in support of the mutation theory than that based on the behavior of *O. Lamarckiana*, a form unknown as the component of any native flora.

The title of a recent paper, "Mutation bei *Œnothera biennis* L.," by T. J. Stomps,[1] a former student of Professor De Vries, naturally then arouses interest especially since he is working with this same *biennis* of the sand dunes of Holland, a type well known to a number of botanists who are conducting experimental studies on œnotheras. A brief discussion of the claims indicated

[1] Stomps, T. J., "Mutation bei *Oenothera biennis* L.," *Biologischen Centralblatt*, XXXII, p. 521, 1912.

by the title of this paper, an analysis of the evidence presented and its possible interpretation supplies the chief incentive for this review.

The greater part of this paper consists of a discussion of certain criticisms directed against the mutation theory by those who believe that *O. Lamarckiana* is of hybrid origin. Certain objections of Stomps appear to the writer well founded, but we shall not take the space to consider this portion of the paper since the greater interest attaches to the value of the direct evidence offered by him in support of the mutation theory.

When we come to the short account of the experimental work of Stomps we find that the so-called "mutants" were not derived from the pure Dutch *biennis* of the sand dunes but from a cross between this race and a type designated *O. biennis cruciata*. This fact seems to the writer of fundamental importance in judging the conclusions of Stomps. It should be made clear that the form "*O. biennis cruciata*" is recognized in the more recent taxonomic treatments as a true species sharply distinguished from types of *biennis* by its floral characters. Whatever may have been the origin of *O. cruciata* or its possible relationship to *O. biennis,* a cross between these types must certainly be regarded as a cross between two very distinct evolutionary lines and its product a hybrid in which marked modifications of germinal constitution are to be expected.

Œnothera cruciata differs from *O. biennis* most conspicuously in having very narrow linear petals, from 1–3 mm. wide, in sharp contrast to the broad heart-shaped petals characteristic of *biennis*. *O. cruciata* is found wild in certain regions of New England and New York and is consequently a native American species. Stomps assumes that the *cruciata* in Holland is a mutant from the Dutch *biennis,* but his belief rests upon no direct evidence. *Cruciata* has never appeared in the extensive cultures of the Dutch *biennis* grown by De Vries and Stomps. Neither have we any direct evidence that the American *cruciata* has come from any form of *biennis*. It is true that the species *cruciata* and *biennis* appear to be closely related, but it is equally clear that they constitute very distinct lines each with a long period of evolutionary independence. I can not see the justification for Stomps's attitude when he treats a cross between the *biennis* and *cruciata* of the sand dunes of Holland as though it were the combination of forms within the same species which have similar germinal constitutions.

Stomps lays emphasis on the purity of his material of *biennis* and *cruciata* which had been carried along for several years in pure lines from original wild plants of the sand dunes. He states that the crossing of these two forms is concerned alone with the floral peculiarities of *cruciata*, since in all other characters the two types are the same. It seems to the writer hardly possible that lines so well established as *biennis* and *cruciata* can be absolutely the same in all respects except that of flower form, although this is obviously the most important point of difference. The American forms of *cruciata* are exhibiting among themselves remarkable differences of germinal constitution.

The observations of Stomps are of interest. He obtained in the second generations from crosses between *biennis* and *cruciata* two marked variants. These are called *biennis nanella* and *biennis semi-gigas* because of the similarity to somewhat corresponding variants from *Lamarckiana*. We are not informed as to the proportions in which these new forms arose, a point of importance since we should like to know whether they are very rare, as say $1:10,000$, or more common.

The first variant, *biennis nanella*, appeared in the second generation of the cross *biennis* $\times$ *cruciata*. This cross gave an F_1 hybrid with heart-shaped petals as in the mother plant; no statements are made as to the size relations. In the F_2 generation there was a splitting into forms of *biennis* and *cruciata;* we are told nothing of the proportions of these individuals in the cultures or of their range of variation. One of the *biennis*-like forms presented a dwarf habit which distinguished it from the *biennis* parent in much the same way that *nanella* is distinguished from *Lamarckiana*. This plant, *biennis nanella,* differed from *Lamarckiana nanella* by the same characters that distinguish *biennis* from *Lamarckiana*. An important point of resemblance to *Lamarckiana nanella* lay in its sensitiveness to bacteria which Zeylstra discovered within the tissues of this type and showed to be responsible for certain abnormal characters. De Vries has shown that *Lamarckiana nanella* grown in a soil treated with calcium phosphate became healthy and Stomps found that his *biennis nanella* responded in a similar way to this treatment.

The second variant, *biennis semi-gigas,* appeared in a second generation from the reciprocal cross *cruciata* $\times$ *biennis*. This cross also gave an F_1 hybrid with flowers of the *biennis* type

and in the F_2 generation there was likewise a splitting of the culture into forms of *biennis* and *cruciata*. One of the *biennis*-like forms presented a more vigorous habit and a larger size of buds, flowers and leaves, suggesting the differences between *Lamarckiana* and its derivative *gigas*. The style was longer than in *biennis* and self-pollination, characteristic of *biennis,* was impossible. This plant proved to be almost sterile.

A count of the chromosomes as shown by mitotic figures in meristematic tissue of young buds determined them to be 21 in number. This important fact placed the plant in that group intermediate between the usual types of *Œnothera* with 14 chromosomes and that very rare variant from *Lamarckiana,* called *gigas,* which has 28 chromosomes. It has recently been shown that certain plants that have been mistaken for *gigas* have 21 chromosomes and for these the name *semi-gigas* has been proposed. Consequently Stomps calls the plant from the cross *cruciata* $\times$ *biennis* with 21 chromosomes *biennis semi-gigas*.

The observation of this remarkable plant and the determination of its chromosome count is a matter of great interest. The fact that the number of the chromosomes (21) is not twice the number of the parent types (14) shows that the germinal variation did not take place after a normal fertilization, for a doubling of the number of chromosomes in the fertilized egg or embryo would give a plant with 28 chromosomes. It indicates that a gamete produced by one of the plants in the F_1 generation had 14 chromosomes and that this element combining with a normal gamete (7 chromosomes) produced this exceptional plant with 21 chromosomes.

I have suggested[2] a way in which gametes of an *Œnothera* might be formed with 14 chromosomes in place of the normal number. The presence of 28 chromosomes instead of the normal number 14, during a heterotypic mitosis in an *Œnothera* might come about from a somewhat earlier appearance of that premature division of the chromosomes which normally takes place as early as anaphase of this mitosis. Thus a pushing forward of this premature fission of the chromosomes from the anaphase to the metaphase of the heterotypic mitosis would result in the distribution of 14 chromosomes to each pole of the spindle. Another fission introduced before the metaphase of the homotypic mitosis would make possible a group of 4 nuclei at the end of the reduc-

[2] *Annals of Botany,* Vol. XXV, p. 959, 1911.

tion divisions each with 14 chromosomes. From such nuclei gametes would be formed with 14 chromosomes.

The position of Stomps is clear. He believes that the Dutch *biennis* and *cruciata* have identical germinal constitutions except for the factors that determine floral structure and therefore with respect to other characters can be crossed as though they were homozygous. Since the cross gave two marked variants which differed from the parents in other respects than those of floral structure these two plants are mutants. These conclusions are then applied by Stomps to the problem of the status of *Lamarckiana* in the following line of reasoning. Since *biennis* mutates and since *biennis* is probably an older species than *Lamarckiana* it follows that mutations among the œnotheras are older than *Lamarckiana* and that consequently the mutations of this species can not be the result of hybridization.

The line of argument rests primarily on the assumption that *biennis* and *cruciata* have exactly the same germinal constitution except for floral characters. This I can not believe possible considering the long evolution back of the two lines. Why did Stomps find it necessary to cross *biennis* with *cruciata* to obtain his ''mutants''? If homozygous in all respects except for flower structure why should not *biennis* alone or *cruciata* alone give the same mutants? From my point of view Stomps really made a cross between two rather closely related species and obtained *first* the segregation of flower types to be expected in the F_2 generation among which from my experience I should expect a wide range of variation, and *second* Stomps obtained two marked variants due to some germinal modification as the result of the cross.

This sort of phenomenon I am obtaining frequently in crosses of my races of American *biennis* and *grandiflora*. The *nanella* condition of dwarfed growth is very common in F_2 generations. And, last summer in an F_3 generation a large plant appeared with leaves so thick and stems, buds and flowers so stocky that I have hardly a doubt but that the cytological examination will show an increase in the number of chromosomes.

In so far as the observations of Stomps bear upon the problem of mutation my interpretation would be exactly the reverse of his. To me they further illustrate the same phenomenon that I am obtaining through my hybrids of *biennis* and *grandiflora*, namely, that behavior by which these hybrids in the F_2 generation

throw off variants that in taxonomic practise would be considered new species readily distinguished from the parents of the cross and from the F_1 hybrid. I have this past summer found that F_2 hybrids similar in character to the F_1 will in the F_3 generation repeat the performance of the F_2 and throw off again some of the same marked variants.

It is a satisfaction to know that De Vries and Stomps stand firmly by the original definition of a mutation as a germinal variation (and this means inheritable) from a pure stock, *i. e.*, from homozygous material. This is a valuable concept whether or not mutation proves to be a rare phenomenon. Furthermore, one of the most important lines of experimental study is that which will endeavor to determine with precision the conditions under which true mutations may arise. There has been a loose usage of the term mutation which should it become prevalent will take from the word the significance described above, and reduce it to a meaning no more precise than that of a marked germinal variation from any source. If the word mutation is to be kept in the sense of De Vries it must be reserved for germinal variations from homozygous stock.

<div style="text-align: right">BRADLEY MOORE DAVIS</div>

A CONVENIENT MICROSCOPE CASE

A VERY convenient case for holding microscopes, especially for large, beginning courses where two or more students in different sections use the same instrument, is shown in the accompanying photograph.

The case here shown was built to stand in a shallow offset in the laboratory near a door, and fills a small space that would otherwise be wasted. As is seen from the numbers below the sections, it will hold fifty standard microscopes. Each instrument has a number on the base to correspond to the number on its respective section. Across the floor of each section, at the back, is nailed a 2 in. $\times$ 2 in. strip of wood to stop the base of the microscope and to serve as a shelf for the extra oculars. Holes of the proper diameter in the shelf would hold these oculars more safely. The doors slide easily on a metal track with ball-bearing wheels and have brass pushes set flush with the surface of the wood. They may be fastened with a catch or with a lock and key.

Below the case proper is a shelf to hold laboratory books. An improvement over the case here shown would be to have two shallow shelves, in place of one, divided into sections for the

further alphabetical distribution of the books. The case here described is 84 inches high, 51 inches wide, and 13 inches deep, outside measurements.

There is wasted, of course, a vertical strip about four inches wide in the center of the case where the doors overlap, but it is always hidden, whether the doors be open or shut.

Such a case, if well made, is practically dust-proof, and is economical not only of space but of money as well, since the cost of the individual microscope boxes may be saved in buying new instruments. A case similar to this has been used by the writer for several years and has proved entirely satisfactory.

ALBERT M. REESE

A LITERARY NOTE ON THE LAW OF GERMINAL CONTINUITY

THE distinctive theory of germinal continuity or continuity of the germ-plasm is, historically speaking, of much more recent origin that the broader doctrine of genetic continuity from which it was derived and with which, in the usage of some writers, it is made synonymous.   Genetic continuity in its widest sense embodies the proposition that "living matter always arises by the agency of preexisting living matter,"[1] and in a more restricted sense means that all living cells must be derived by continuous lineage from the cells of preexisting generations.   The theory of germinal continuity, in its most highly developed form, conceives the germinal protoplasm as dividing into two portions, from one of which the somatic or body cells of the offspring are developed while the other portion is reserved unchanged for the formation of the reproductive material of the adult individual.   The general doctrine of continuity is fundamentally essential to both these theories, but germinal continuity, at least in any Weismannian sense, always involves the further assumption of a transmission from generation to generation of an unmodified residue of the specially organized germinal substance, the germ-plasm, through a definite series of cells, but this concept does not imply that there is necessarily a direct connection between the germ-cells of consecutive generations.

To Richard Owen the credit is usually given of being the first to recognize the distinction between body-cells and germ-cells and thus to foreshadow the idea of germinal continuity. Writing in 1849, he said:

Not all the progeny of the primary impregnated germ-cell are required for the formation of the body in all animals: certain of the derivative germ-cells may remain unchanged and become included in that body which has been composed of their metamorphosed and diversely combined or confluent brethren: so included, any derivative germ-cell or the nucleus of such may commence and repeat the same processes of growth by imbibition, and of propagation by spontaneous fission, as those to which itself owed its origin; followed by metamorphoses and combinations of the germ-masses so produced, which concur to the development of another individual; and this may be, or

[1] Huxley, T. H., "Lay Sermons, Addresses and Reviews," New York, 1870, p. 350.

may not be, like that individual in which the secondary germ-cell or germ-mass was included.

When the primary division of the impregnated germ-cell takes place, it must divide its properties with its matter between the two cells resulting from the spontaneous fission of its nucleus: and this result must follow every subsequent division. It is scarcely figurative therefore to say that the primary or parent germ-cell has equally divided its spermatic virtue amongst its countless progeny.[2]

Owen's suggestions apparently received no consideration and were later disregarded by the author himself. Somewhat similar ideas were expressed by Haeckel[3] in some of his earlier speculations. Galton, says Weismann,[4] was the first to express ideas resembling the theory of germinal continuity, but these ideas were later considerably modified.[5]

A clear expression of the conception of germinal continuity is found in the writings of Jäger, but his ideas made little impression, and inaccurate citation of his work has sometimes caused his disparagement. In 1877, restating previously expressed propositions, he said:[6]

The basis of heredity consists in this, that throughout whole series of generations the germ-protoplasm of animals retains unchanged its specific quality in spite of all external influences. In the actual ontogeny the available germ-protoplasm may divide into two groups, the *ontogenetic,* from which the existing individual is formed, and the *phylo-*

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[2] Owen, Richard, "On Parthenogenesis," London, 1849, pp. 5–6, 63–64.

[3] Haeckel, E., "Generelle Morphologie," 1866, pp. 287–289.

[4] Weismann, A., "The Germ-plasm, A Theory of Heredity," New York, 1902, p. 198.

[5] Galton's early ideas were expressed as follows:

"From the well-known circumstance that an individual may transmit to his descendants ancestral qualities which he does not himself possess, we are assured that they could not have been altogether destroyed in him, but must have maintained their existence in a latent form. Therefore each individual may properly be conceived as consisting of two parts, one of which is latent and only known to us by its effects on his posterity, while the other is patent, and constitutes the person manifest to our senses.

"The adjacent and, in a broad sense, separate lines of growth in which the patent and latent elements are situated, diverge from a common group and converge to a common contribution, because they were both evolved out of elements contained in a structureless ovum, and they, jointly, contribute the elements which form the structureless ova of their offspring."—Galton, F., "On Blood-relationship," *Proceedings of the Royal Society of London,* Vol. 20, 1872, p. 394.

[6] Jäger, G., "Physiologische Briefe," *Kosmos,* Jahrg. I, Bd. I, 1877, p. 17.

genetic, which is reserved until the time of puberty for the formation of the reproductive material. This reservation of the phylogenetic material I designated as the Continuity of the Germ-protoplasm.[7]

This clear expression of the doctrine of germinal continuity apparently does not appear in Jäger's later work,[8] to which reference is usually made.

Weismann in his essay on the "Continuity of the Germ-plasm,"[9] assumed that he was the first to give expression to this conception but in a later work[10] made acknowledgments to other authors who had anticipated his theory. With respect to Jäger, however, he said:[11]

The praiseworthy attempt to do justice to my predecessors in this particular subject has perhaps been carried too far. In Geddes and Thompson's "Evolution of Sex" (p. 93), for instance, a quotation is given from Jäger which seems to prove that he anticipated me with regard to the theory under consideration. The quotation in which this idea is expressed is, however, not taken from the book published in 1878 but from an essay written ten years later, and it concludes with the following words: "This reservation of the phylogenetic material I described as *the continuity of the germ-plasm.*" But no mention is made by Jäger of the continuity of the germ-plasm in his book which ap-

[7] The original language of these statements is as follows: "In der 'Zeitschrift für wissenschaftliche Zoologie' Bd. XXVII habe ich unter den Titel 'Ueber die Bedeutung der Geschmak- und Geruchstoffe' ein Erörterung der chemischen Seite der Vererbungsfrage gegeben, nachdem ich schon vorher in meinen 'Zoologischen Briefen' der physikalische Seite einige Betrachtungen gewidmet hatte. Ich will es um Folgenden versuchen, dieser Frage einige neue Anhaltspunkte abzugewinnen und das dort Gesagte zu ergänzen.

"Meine früheren Auseinandersetzungen gingen dahin: Das Fundament der Vererbung besteht darin, dass durch grosse Reihen von Generationen hindurch das Keim Protoplasma eines Thieres eine sich stets gleichbleibende spezifische Beschaffenheit allen Anfechtungen von aussen zum Trotz bewahre. Ich sagte: Bei der jedesmaligen Ontogenese scheide sich das verfügbare Keimprotoplasma in zwei Gruppen, die *ontogenetische,* aus welcher das jeweilige Individuum aufgebaut wird und die *phylogenetische* welche reservirt werde, um zur Zeit der Geschlechtsreife die Fortpflanz-ungstoffe zu bilden. Diese Reservirung des phylogenetischen Materials bezeichnete ich als Continuität des Keimprotoplasmas."

[8] Jäger, G., "Lehrbuch der allgemeinen Zoologie," Leipzig, 1878, II Abtheilung.

[9] "Der Continuität des Keimplasmas," Jena, 1885; Essay IV in author-ized translation, 2d ed., 1891, p. 163.

[10] "The Germ-Plasm, A Theory of Heredity," New York, 1902, pp. 198–202.

[11] *L. c.,* p. 200, footnote.

peared in 1878, in which a connection between the germ-*cells* of different generations is supposed to exist:—and this is not the case. The entirely new statement of his ideas has been influenced by those contained in my essays which had appeared in the meanwhile.

As a matter of fact the quotation from Jäger which Weismann repudiates actually appeared more than eight years before the publication of Weismann's essays, as the quotation from *Kosmos*, given above, clearly shows. Although Jäger coined the expression "Continuity of the Germ-plasm," the idea involved seems to have attracted no attention until after the essays of Weismann had aroused general scientific interest.

Jäger also assumed a material connection between the germ-*cells* of different generations,[12] and, in what Weismann characterizes as "a few casual remarks," Rauber[13] expressed a conception which some authors interpret as the same idea.

In the account of his exhaustive researches on the differentiation of the reproductive cells Nussbaum gave clear expression to the doctrine of the continuity of the germ-*cells*, which in a strict sense means that germ-cells arise directly from one another. The views held by Nussbaum[14] were in part set forth in the following words:

[12] See preceding quotations from Weismann.

[13] Rauber, A., "Formbildung und Formstörung in der Entwicklung von Wirbelthieren," *Morphologische Jahrbuch*, Vol. 6, 1880, p. 4. The "casual remarks" are as follows:

"Die beiden Theilstücke, deren Verbindung das neue Wesen bewirkt, sind bei den höheren Thierformen enthalten in besonderen Organen, den Keimdrüsen. Da aber die Keimdrüsen die folgende Generation beherbergen, so erscheint ein Individuum als der Träger zweier Generationen, seiner eigenen sowie der folgenden Generation. Insoweit er der Träger seiner selbst ist, stellt er eine Person im engeren Sinne dar; er ist der *Personaltheil* der dualistischen Anlage. Die Träger der Zukünftigen Generation, die Keimdrüsen, stellen dagegen den *Germinaltheil* der dualistischen Anlage dar.

"Personal- und Germinaltheil gehen aber von *einem* befruchteten Ei aus, *ein* solches Ei enthält den Stoff mit dem Kräfteplan zu der genannten dualistischen Anlage. Man kann darum auch von einem Personaltheil und Germinaltheil des befruchteten Eies reden."

[14] Nussbaum, M., "Zur Differenzierung des Geschlechts im Thierreich," *Archiv für mikroskopische Anatomie*, Bd. 18, 1880, p. 112. The text of the original is worded thus:

"Es theilt sich demgemäss das gefurchte Ei in das Zellenmaterial des Individuums und in die Zellen für die Erhaltung der Art. In beiden Theilen geht die Zellenvermehrung continuirlich weiter; nur tritt im Leibe des Individuums die Arbeitstheilung hinzu, während in seinen Geschlechtszellen sich eine einfache additionelle Theilung vollzieht. Die beiden Zellen-

The segmented ovum divides into the cell-material of the individual and into the cells for the preservation of the species. In both divisions the cell-multiplication proceeds continuously, but in the body of the individual division of labor occurs, while in the reproductive cells simple division only takes place. Both groups of cells and their offspring are propagated quite independently of each other, so that the reproductive cells have no share in the development of the tissues of the individual, and no seminal or ovicular cell arises from the cell-material of the individual. After the segregation of the reproductive cells the history of the individual and that of the species are entirely distinct, and because of this relation the " constancy " of the species is more easily understood; that is, the sharp persistence of the phenomenon of atavism by means of which ancestral traits are transmitted. For sperm and ovum are not derived from the cell-material of the parent organism, but have a common origin with it. However, since they are preserved within it, they are subject to the conditions which modify the parent organism; therefore the transmission of " acquired " characteristics is not excluded.

Nussbaum is said by some to be the first to suggest the idea of the cellular continuity of successive generations, but this conception is clearly implied in Virchow's aphorism[15] "omnis cellula a cellula," and was fully stated in 1858 in the Law of Genetic Cellular Continuity first clearly formulated by Virchow[16] as follows:

Just as an animal can originate only from an animal and a plant only from a plant, so every cell must arise from a preexisting cell. Although there are individual cases in which strict proof is still wanting, yet the principle is firmly established that for all living beings, whether they be entire plants or animal organisms or integrant parts of the same, there exists an eternal law of *continuous development.*

gruppen und ihre Abkömmlinge vermehren sich aber durchaus unabhängig von einander, so dass die Geschlechtszellen an dem Aufbau der Gewebe des Individuums keinen Antheil haben, und aus dem Zellenmaterial des Individuums keine einzige Samen- oder Eizelle hervorgeht. Nach der Abspaltung der Geschlechtszellen sind die Conti des Individuums und der Art völlig getrennt, und wir glauben aus diesem Verhalten die 'Constanz' der Art, d.h. die in der Erscheinung des Atavismus gipfelnde Zähigkeit, mit der sich die Eigenthümlichkeiten der Vorfahren vererben, begreiflicher zu finden. Denn Samen und Ei stammen nicht von dem Zellenmaterial des elterlichen Organismus ab, sondern haben mit ihm gleichen Ursprung; da sie aber in ihm aufbewahrt werden, so sind sie auch den Bedingungen unterworfen, welche auf den elterlichen Organismus modificirend einwirken, weshalb die Vererbung der 'erworbenen' Eigenschaften nicht ausgeschlossen ist.''

[15] *Archiv für Pathologische Anatomie*, Bd. 8, 1855, p. 23.

[16] ''Die Cellularpathologie im ihrer Begründung auf physiologische und pathologische Gewebelehre,'' Berlin, 1858, p. 25.

On the other hand, to Nussbaum is sometimes credited the theory of germinal continuity, but in such cases authors apparently do not sharply distinguish continuity of the germ-*plasm* from continuity of the germ-*cells*. Thus Minot[17] says:

We owe to Moritz Nussbaum the theory of germinal continuity—the only theory of heredity which seems tenable at the present time. According to this theory, the germ-cells are set aside during the segmentation of the ovum and preserve the essentially undifferentiated qualities of the protoplasm and nucleus of the ovum, from the division of which they arise.

However, irrespective of the conclusions that may be reached as to whom priority in the statement of the theory of germinal continuity belongs, it is to Weismann that credit must be given for the development of this doctrine into an important theory of heredity.

There would seem to be a gain in precision and clearness of expression in discussions involving the idea of continuity in development if a distinction were always made between (1) *genetic continuity, or biogenesis,* (2) *genetic cellular continuity,* (3) *continuity of the germ-cell* and (4) *germinal continuity.* Thus restricted the term germinal continuity expresses more closely the conception held by the greatest exponent of this theory. Since Jäger first used the phrase ''Continuity of the Germ-plasm'' I suggest that his name be linked with that of Weismann in referring to this principle, which may well be called the Jäger-Weismann Law of Germinal Continuity, the esential doctrine of which is thus expressed:[18]

In each ontogeny, a part of the specific germ-plasm contained in the parent egg-cell is not used up in the construction of the body of the offspring, but is reserved unchanged for the formation of the germ-cells of the following generation.

However, the real significance of Weismann's theory of germinal continuity and its bearing on theories of heredity can not be fully appreciated without at least a general acquaintance with the somewhat voluminous literature of this subject.

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[17] Minot, C. S., ''Laboratory Text Book of Embryology,'' Philadelphia, 1910, p. 28.

[18] Weismann, A., ''Essays upon Heredity and Kindred Biological Problems,'' authorized translation, 2d edition, Oxford, 1891, p. 170.